MORPHOLOGICAL OBSERVATIONS ON *DINOPHYSIS* SPECIES (DINOPHYCEAE) FROM MEDITERRANEAN COASTAL WATERS

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ABSTRACT — Morphological aspects of various *Dinophysis* species (e.g. *D. sacculus*, *D. fortii* and *D. acuminata*) collected from Mediterranean coastal areas (southern Italy) are described. Data on the fluorescence of *Dinophysis* are given in addition to cell details in scanning electron and light microscopy.

Specimens of *D. sacculus* from Tyrrhenian brackish waters, where this species has been associated with slight DSP -- toxicity of mussels, display high variability in cell shape and size, whereas the thecal ornamentation has a regular pattern. Cells of *D. sacculus*, as well as *D. acuminata* from the Straits of Messina, autofluoresce bright red and yellow — orange, indicating the possible presence of both chlorophyll and phycobilin pigments. Globular components similar to food vacuoles, were observed inside a few specimens of the *D. acuminata* complex and in *D. rotundata* cells, further supporting the respective mixotrophic capability and the heterotrofic behaviour of these dinoflagellates.

RÉSUMÉ — Les aspects morphologiques de diverses espèces de *Dinophysis* (par ex. *D. sacculus*, *D. fortii* et *D. acuminata*) prélevées dans les zones côtieres de la Mer Mediterraneé (Italie méridionale) sont décrites.

Les données concernants la fluorescence de *Dinophysis* sont fournies, avec en plus des détails de la cellule en microscopie électronique à balayage et photonique.

Les échantillons de *D. sacculus* des eaux saumâtres de la Mer Tyrrhénienne, où cette espèce a été associée à la toxicité DSP des coquillages, montrent une grande variabilité de forme et de dimension cellulaire, tandis que l'ornementation de la thèque montre un dessin régulier. Les cellules de *D. sacculus*, ainsi que celles de *D. acuminata* du Détroit de Messine, ont une fluorescence rouge et jaune — orange, indiquant la présence possible aussi bien de chlorophylle que de phycobilines. Des globules semblables à des vacuoles digestives ont été observés à l'intérieur de quelques exemplaires du complexe *D. acuminata* et de *D. rotundata*, confirmant ainsi la respective capacité mixotrophique et le comportment hétérotrophe de ces dinoflagellés.

KEY-WORDS *Dinophysis*, morphology, Mediterranean Sea.

INTRODUCTION

Numerous species of *Dinophysis* Ehrenberg have been associated with DSP (Diarrhetic Shellfish Poisoning) in diverse geographical areas (e.g. Dahl & Yndestad, 1985; Lassus *et al.*, 1985; Sampayo *et al.*, 1990; Yasumoto, 1990; Delmas *et al.*, 1992; Boni *et al.*, 1993). The production of toxic metabolites, okadaic acid (OA) and its derivatives such as dinophysistoxins (DTXn), and occasionally pectenotoxins (PTXn), has however been proved only in a limited number of species, i.e. *D. acuminata*, *D. acuta*, *D. fortii*, *D. mitra*, *D. norvegica*, *D. sacculus*, *D. tripos* and, despite controversial opinions, for *D. rotundata* (Cembella, 1989; Lee *et al.*, 1989; Masselin *et al.*, 1992). This is probably due to low cell densities in coastal waters and unsuccessful attempts to cultivate this dinoflagellate genus so far.

First experimental studies seemed to evidence the capability of *Dinophysis acuminata* and *D. fortii* to prey upon cryptomonads (Ishimaru *et al.*, 1988) and the presence of food vacuoles and mixotrophy were shown for some photosynthethic species (*D. acuminata*, *D. norvegica*) (Jacobson & Andersen, 1994). Hallegraeff and Lucas (1988) also distinguished morphotypes *Dinophysis* and *Phalacroma* on the basis of physiological and ecological criteria, although the presence or absence of chloroplasts (or phagocyted algal particles) cannot be considered [illegible] a distinctive character for both genera. Within the genus *Dinophysis* (*sensu stricto*), in fact, species lacking chlorophyll or containing cyanobacteria-like endosymbionts were reported, in addition to species with chloroplasts (Lessard & Swift, 1986).

Another aspect of *Dinophysis* (e.g. the *D. acuminata* complex) is the high variability in cell shape and size, which may vary according to the site and the season (Solumn, 1962). Changes in cell shape induced by the presence of food vacuoles and sexual dimorphism (Hansen, 1993) also complicate the species taxonomy.

Morphological observations on *Dinophysis* specimens selected from Mediterranean coastal waters are presented in this paper. Major attention is given to the thecal features of *D. sacculus* from a Tyrrhenian lagoon where spring blooms of this species have been associated with slight DSP-toxicity of experimentally contaminated mussels (Giacobbe *et al.*, 1995).

METHODS

Dinophysis cells were collected between 1988 and 1993 from the upper waters (0-5 m layer) of some Mediterranean areas: a Tyrrhenian lagoon of Sicily (Oliveri Bay, Gulf of Patti — 38°08′ N, 15°03′ E, April 1988 and April 1993); the harbour of Augusta, Ionian Sea (37°12′ N, 15°03′ E, March-August 1989); the coastline of Calabria (38°-40° N, 15°30′-17°30′ E, March 1991 and September 1993); the Straits of Messina (38°10′ 38°13′ N, 15°35′-15°39′ E, July 1992).

Samplings were made using standard and Apstein nets (mesh: 40 and 20 µm, respectively) and/or Go-Flow Niskin bottles (General Oceanics). Most of the cells were preserved with neutralized formaldehyde (final concentration: 2 %) and examined by light microscope (Axiovert-35 Zeiss) equipped with a Contax 167MT camera. Brightfield or phase contrast light microphotographs were taken with Agfa PAN-F film, after cell staining with 1 % solution of Trypan blue.

Part of the fixed cell concentrates were washed with bidistilled water to remove salt crystals, passed over stubs, air-dried, sputter coated with gold and examined by Hitachi S-800 scanning electron microscope (University Policlinic, Messina) or Hitachi S-4000 field emission SEM ("La Sapienza" University, Rome). SEM observations were made operating at accelerating voltages of 30 and 2-5 kV, respectively.

Some *Dinophysis* samples were preserved with glutaraldehyde (1 %), stored in the dark at 4°C and examined by epifluorescence microscopy using an Axioplan and Zeiss filter set 487910 (BP 450-490 exciter filter, FT 510 chromatic beam splitter, BP 515-565 barrier filter).

RESULTS AND DISCUSSION

Micromorphometry of *D. sacculus* from Tyrrhenian brackish waters

Figure 1 shows the general morphology of *D. sacculus* Stein cells from Tyrrhenian waters (Green Pool, Oliveri Lagoon), whose salinity ranges from April to September, when this species is present, between 21 and 26 ppt (ITME, 1991).

The majority of specimens selected from the area have a total length within the size range of 48-60 µm, reported by Schiller (1933) for *D. sacculus*, whereas 35 % of the cells encountered slightly exceeds the above range. On average, the total cell length is 59 ± 3 µm ($\bar{x}$ ± SD) (n = 50; coefficient of variation = 6 %), being greater than that described for *D.* cf. *sacculus* from French coastal areas (Lassus & Bardouil, 1991). This observation agrees with previous studies on other *Dinophysis* species, showing how salinity influences the cell size. Solumn (1962) found that *D. acuminata* cells were longer in areas of low salinity, which was also noted by Matzenauer (1933) for some *Dinophysis* species belonging to the *caudata* group. Recent findings from the Galician Rias Baixas (NW Spain) also evidence changes in cell shape and size of *D. acuminata* in response to variations in environmental conditions, with smaller cells at higher values of salinity (34.5-35.5 ppt) and temperature (Bravo *et al.*, 1995a)

The average cell width of the specimens from the brackish area is 29 ± 3 µm (n = 21; c.v. = 11 %) and the length/ width ratio: 1.8 ± 0.1 (n = 10). The cell wall has the following characteristics: straight, slightly concave or convex dorsal margin (Figs 1A, 22), rounded antapex, with a few to numerous knobs of irregular size (Fig. 1C), flattened or slightly convex (similar to *D. acuminata*) ventral posterior margin (Figs 1A, 1C, 22), left sulcal list (lsl): 31 ± 3 µm in size (n = 20; c.v. = 9 %), smooth, with straight or turned downwards posterior rib (R3) (Fig. 1B) and right sulcal list (rsl) curved in outline and extending beyond the middle rib (R2) of the left list (Fig. 2) (rsl = 0.5 lsl in length).

The cell concentrations of *D. sacculus* found in this area reach high values (max. 40000 cells l^{-1} in 1988 and 8000 cells l^{-1} in 1993) when compared to other coastal zones of Sicily, where *Dinophysis* spp. were reported in very low amounts (Giacobbe & Maimone, 1991; Giacobbe *et al.*, 1991). ELISA tests on mussels introduced in the lagoon as bioassay organisms, coupled with microscopical analysis of midgut contents, showed a spring OA-production by this species, even if at low levels (Giacobbe *et al.*, 1995). However, there is no information on the possible relationships between environmental conditions and changes in toxigenicity of this strain. The same species, together with other *Dinophysis* spp. (e.g. *D. fortii*, *D.* cf.

acuminata) has also been associated with DSP-toxicity of mussels in diverse areas of the Northern Adriatic Sea (e.g. Boni *et al.*, 1992; Della Loggia *et al.*, 1993).

A few cells of *D. sacculus* (15 % of the whole population) have a markedly concave dorsal margin (Fig. 23), as also observed by Sidari *et al.* (1995) in coastal waters of the Gulf of Trieste (Northern Adriatic Sea). However, this characteristic — included by Schiller (1933) among the morphological features of *D. sacculus* — was afterwards reported as belonging to *D. pavillardi* Schroeder (see Lassus & Bardouil, 1991). Although there is no real evidence of a specific difference between *D. sacculus* and *D. pavillardi*, the prevailing of one morphotype over the other may have ecological significance, since this is probably related to specific environmental conditions (Bravo *et al.*, 1995b).

No couplet of cells connected by a megacytic dorsal bridge, resulting from vegetative cell division, was observed among the specimens of *D. sacculus* from the Tyrrhenian area. Neither were there stages of sexual reproduction, i.e. couplets of cells of diverse size, joined along the ventral edge, as observed for specimens of *Dinophysis* cf. *acuminata* from Port Underwood, New Zealand (Mackenzie, 1992).

Figures 3 and 4 show the plate ornamentation of *D. sacculus*. The thecal plates are sculptured with a circular areolation; within the cingulum, as well as just behind the posterior cingular list (pcl), pores are arranged in a row, whereas they are unevenly and more widely spaced in the rest of the hypotheca. Here, areoles with pores are sometimes replaced by shallow pits (Fig. 3).

On the whole, cells of *D. sacculus* from this population display variable cell shape and size; in contrast, the surface architecture of the theca has a basic pattern remarkably similar in all the specimens examined.

Dinophysis spp from the Ionian Sea and the Straits of Messina: main interspecies differences

The pattern of thecal ornamentation of *D. sacculus* is shared by other species of *Dinophysis*, e.g. *D. acuminata* Claparède et Lachmann, *D. acuta* Ehrenberg, *D. caudata* Saville-Kent, *D. norvegica* Claparède et Lachmann, *D. fortii* Pavillard (see Hallegraeff & Lucas, 1988). Cells of the latter species have, however, a more prominent circular areolation of the theca when seen by scanning microscopy (Figs 5, 6), as observed on samples from the coastline of Calabria and the bay of Augusta (Ionian Sea); a decoration of the left sulcal list of *D. fortii* is also visible by LM. These characteristics, as well as the general cell shape (Fig. 12) (with convex dorsal margin), and size (60-70 µm – Balech, 1976), point towards the specific identification, although a wide variation in minor features has led to some confusion as to the limits of *Dinophysis* species. A number of distinct internal components have been described by Lucas & Vesk (1990) for specimens of *D. fortii* and the closely related species *D. acuminata* from Tasmania, e.g. the nucleus location, at the antapex in the former species and at the apex in the latter and a higher number of chromatospheres (i.e. chloroplasts of senescent cells aggregated in spherical clumps) in *D. fortii*. In the same way, chloroplasts appear scattered throughout the cytoplasm in couplets of *D. caudata* (Fig. 9), which are commonly found in the bay of Augusta, whereas single cells of the variety *caudata*, as well as var. *acuminiformis*, display chloroplasts aggregated in three to four chromatospheres (Figs 14, 15). In contrast to Lucas & Vesk's findings, no chloroplast arrangement in spherical groups is visible in cells of *D. fortii* and *D. acuminata* (Fig. 16) from the Ionian Sea and the Straits of Messina respectively; in the latter species, the nucleus is often located half-way between apex and antapex, close to the dorsal suture (Fig. 17), whereas in some specimens it covers part of the central cell area. Numerous globular components of uniform size, can be observed inside a few small cells of *D. acuminata* from the Straits. Such globules are scattered throughout the cytoplasm and resemble the food vacuoles described by Jacobson & Andersen (1994) for *Dinophysis* spp. from Boothbay Harbor (Maine) and Vancouver; they are more clearly visible in some larger-sized specimens of the *D. acuminata* complex (Figs 18, 19) from the same area. The latter cells are intermediate, in the general morphology, between *D. acuminata* and *D. sacculus*, being similar to *D.* cf. *acuminata* specimens from Quiberon, France (see Lassus & Bardouil, 1991/Fig. 1f). Food vacuoles were also reported by Jacobson & Andersen for heterotrophic species like *D. rotundata* Claparède et Lachmann, which feeds on ciliates using a peduncle, through a process known as myzocytosis (see Schnepf & Deichgraber, 1983; Hansen, 1991). The majority of *D. rotundata* cells found in coastal waters of the Ionian Sea, apparently lack vacuoles, but some specimens clearly display numerous large food vacuole-like globules (Figs 20, 21). The pattern of surface sculpturing of *D. rotundata* is given by shallow depressions and by some pores distributed all over the theca, whereas closely spaced pores border the cingulum (Figs 7, 8).

Table I summarizes the autofluorescence properties of most of the *Dinophysis* species encountered in this study. Under epifluorescence blue excitation, *D. acuminata, D. pavillardi* and *D. sacculus* show red and yellowish primary fluorescence, indicating the possible presence in each cell of chlorophyll and phycobilin pigments, but no cyanobacteria
were found as endosymbionts. *D. caudata* and *D. fortii* fluoresce red, whereas *D. rotundata*, *D. doriphora* (Stein) Abé (Fig. 11) and *D. mitra* (Schutt) Abé (Fig. 10) from the Ionian Sea exhibit a widespread greenish-yellow or green fluorescence, which further confirms the heterotrophic behaviour of these dinoflagellates previously ascribed to the genus *Phalacroma*.

Cells of *D. rotundata, D. doriphora* and *D. mitra* are also present in the Straits of Messina where a high species diversity can be observed in summer. Four other *Dinophysis* spp., i.e. *D. caudata, D. pusilla* Joergensen, *D. sacculus* and *D. schuettii* Murray and Whitting, and other dinophysoid dinoflagellates (e.g. *Ornithocercus magnificus*) were in fact found in July 1992 in this area, which is characterized by high hydrodynamism.

All the species present in the Straits and in the Ionian Sea, including *D. schroederi* Pavillard (Fig. 13) from the bay of Augusta, never exceed cell densities of 2000 cells l^{-1}, with the highest concentrations during the summer season. This is consistent with other observations from the Adriatic Sea (e.g. Cabrini *et al.*, 1995). In contrast, marked blooms of *Dinophysis* (e.g. *D. sacculus*) — and sometimes of other potentially-toxic dinoflagellates (Giacobbe & Maimone, 1994; Giacobbe *et al.*, in press) — occur in lagoon waters of Sicily, often developing during spring. Additional data are however needed to establish the toxigenicity of these dinoflagellate strains and its possible associations with environmental factors.

Table I. Autofluorescence of *Dinophysis* species selected from diverse Mediterranean areas.

Species	Site	Fluorescence
Dinophysis acuminata Claparède et Lachmann	Sicily (The Straits of Messina)	° Bright red and yellow
D. caudata Saville-Kent	Harbour of Augusta (Ionian Sea)	° Red
D. doriphora (Stein) Abé	Harbour of Augusta (Ionian Sea)	* Greenish-yellow
D. fortii Pavillard	Calabria (Ionian Sea)	° Red
D. mitra Schutt	Harbour of Augusta (Ionian Sea)	* Greenish
D. pavillardi Schroeder	Oliveri Lagoon (Tyrrhenian Sea)	° Red and yellow-orange
D. rotundata Claparède et Lachmann	Calabria (Ionian Sea)	* Greenish-yellow
D. sacculus Stein	Oliveri Lagoon (Tyrrhenian Sea)	° Red and yellow-orange

(°) chloroplasts ; (*) no visible chloroplasts

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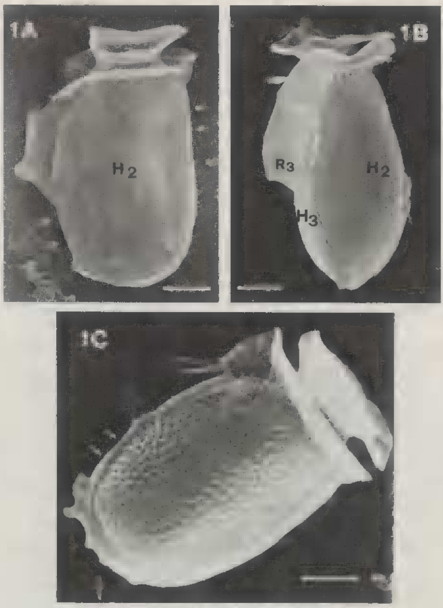
CAPTIONS TO FIGURES

Fig. 1 — SEM. Specimens of *Dinophysis sacculus* from Tyrrhenian brackish waters (Green Pool, Sicily). Scale bars = 10 µm.
(A) Left lateral view. Cell with flattened dorsal and posterior ventral margins (arrows). H2 = left dorsal hypothecal plate. (B) Ventral view. The left sulcal list is supported by straight R3 rib. H3 = right dorsal hypothecal plate. (C) Another specimen (left lateral view) with numerous antapical knobs; the posterior ventral edge is slightly convex (arrows).

Figs 2-8 — Thecal features of *Dinophysis* species. Bars = 2 µm.
SEM. (2) Right lateral view. Theca of *D. sacculus* showing the right list of the sulcus (rsl) and the circular areolation. (3) Enlarged detail of the above specimen with some areoles devoid of pores (arrowheads). (4) Ornamentation within the cingulum and behind the posterior cingular list (pcl) in another cell of *D. sacculus*.
FE-SEM. (5) Thecal ornamentation of *Dinophysis fortii* (Calabria, Ionian Sea) within the cingulum, with a visible double row of poroids, and (6) in the hypotheca. The circular marking is more prominent than in *D. sacculus*. acl = anterior cingular list. (7) *D. rotundata* from coastal waters of Calabria (Ionian Sea). Cell with visible E2 epithecal plate. (8) Detail of *D. rotundata* showing the faint thecal marking.

Figs 9-15 — LM. *Dinophysis* spp. from the bay of Augusta (Ionian Sea). Scale bars = 20 µm.
(9) Couplet of *D. caudata* with daughter cells still attached by the megacytic bridge (10) *D. mitra*. (11) *D. doriphora*. (12) *D. fortii*. (13) *D. schroederi*. (14-15) Single cells of *D. caudata* var. *acuminiformis* and var. *caudata* with chloroplasts aggregate in chromatospheres (arrows).

Figs 16-23 — LM. *Dinophysis* spp. Bars = 20 µm. (16) Small *D. acuminata* cell from the Straits of Messina. (17) Another specimen of *D. acuminata* depicting the nucleus location (arrowheads). (18-19) Cells of *D.* cf. *acuminata* from the Straits and (20-21) *D. rotundata* (Ionian Sea) containing numerous food vacuole-like globules (two focal planes). (22) Morphotypes of *D. sacculus* with diverse cell shape and size (Green Pool, Sicily). (23) *D. pavillardi* from Green Pool, Sicily.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H2
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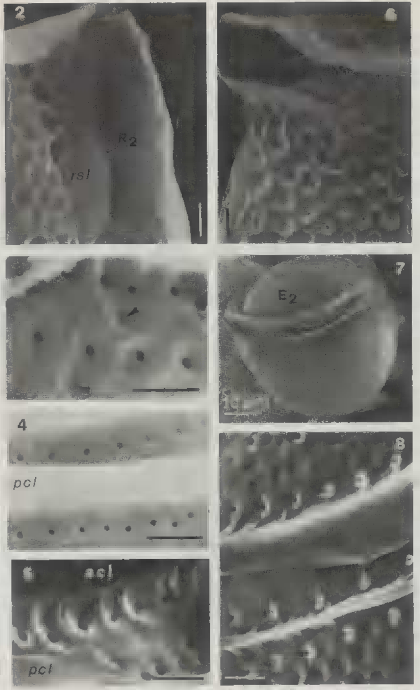
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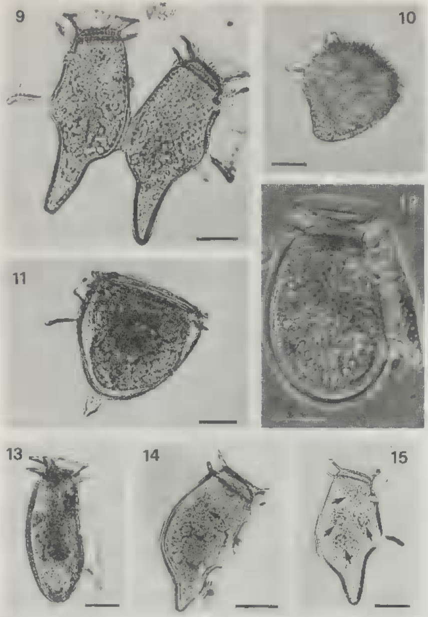
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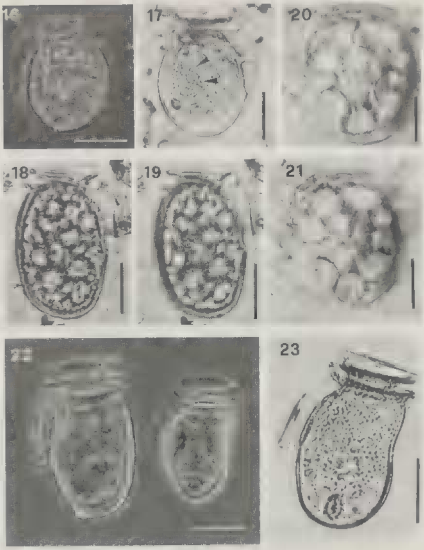
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